

## SHORT COMMUNICATION

### IS THE HAIRY GROOVE IN THE GIBBOSUS MALE MORPH OF *OEDOTHORAX GIBBOSUS* (BLACKWALL 1841) A NUPTIAL FEEDING DEVICE?

**Danny Vanacker, Liesbeth Maes, Sylvia Pardo, Frederik Hendrickx:** Laboratory of Animal Ecology, Zoogeography and Nature Conservation, Ghent University, Ledeganckstraat 35, 9000 Ghent, Belgium, E-mail: Danny.Vanacker@rug.ac.be

**Jean-Pierre Maelfait:** Laboratory of Animal Ecology, Zoogeography and Nature Conservation, Ledeganckstraat 35, 9000 Ghent, Belgium; Institute of Nature Conservation, Kliniekstraat 25, 1070 Brussels, Belgium

**ABSTRACT.** *Oedothorax gibbosus* (Blackwall 1841) (Erigoninae, Linyphiidae, Araneae) is a dwarf spider characterized by dimorphic males. There is a “gibbosus” male morph characterized by a hunch on the posterior third of the carapace, anterior to which is a hairy groove, and a “tuberosus” morph without these features. We observed several gustatorial courtship interactions by a gibbosus male morph and a conspecific female as well as a by a gibbosus male and a male of the closely related species, *Oedothorax fuscus* (Blackwall 1834). These interactions suggest that the hairy groove in the gibbosus male morph is a nuptial feeding device possibly under the influence of sexual selection. The interspecific interactions can possibly be interpreted as ‘robbings’ of the nuptial feeding. The interspecific interactions indicate that the cephalic structure of gibbosus probably does not function as a “lock and key” mechanism.

**Keywords:** *Oedothorax gibbosus*, *Oedothorax fuscus*, interspecific courtship, nuptial feeding, gustatorial courtship

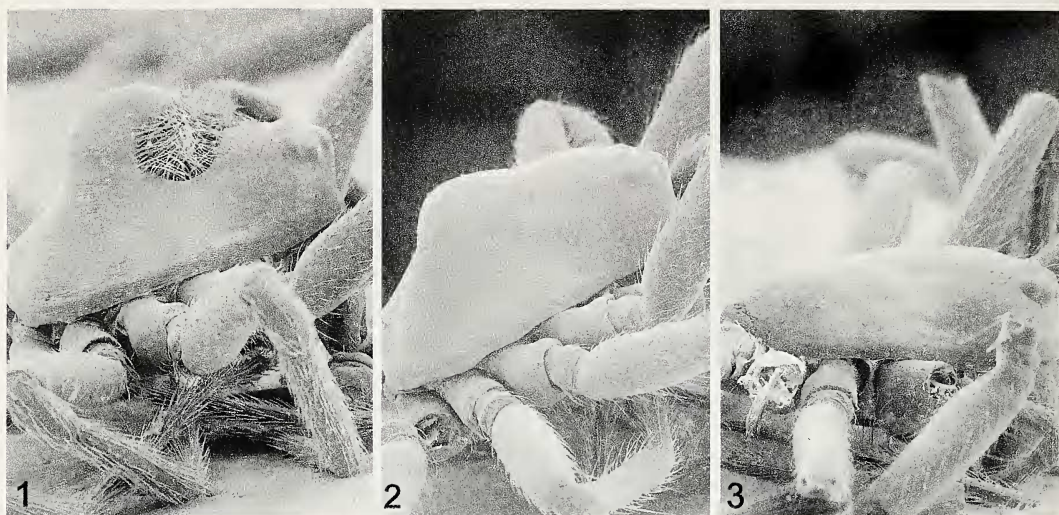
*Oedothorax gibbosus* (Blackwall 1841) is a rare dwarf spider species in Flanders (northern part of Belgium) that occurs only in wet to very wet habitats (De Keer & Maelfait 1989; Maelfait et al.; 1998) such as oligo- and mesotrophic alder carrs. It lives between leaf litter and mosses in the immediate vicinity of open water. These habitats have become scarce in Belgium and therefore this species is known only from a few nature reserves, such as the public nature reserve “Het Walenbos” at Tielt-Winge (50° 55' NL, 4° 51' EL), 30 km north-east of Brussels, where our material was gathered.

*Oedothorax gibbosus* is a species with dimorphic males. In the gibbosus morph the carapace is raised in the foveal region to form a hunch. Between that protuberance and the eye region is a transverse groove surrounded and filled with long black and stiff hairs (Fig. 1). The tuberosus morph (Fig. 2) does not show any remarkable differentiation at the dorsal side of the carapace. Its carapace is only a bit more raised and convex than that of the female (Fig. 3), but lacks the deep notch and the long hairs. Voucher specimens of one *O. gibbosus* female, one gibbosus and tuberosus male morph and one male

of *O. fuscus* are deposited in the collection the Royal Belgian Institute of Natural Sciences, Vautierstraat 29, Brussels, Belgium: IG29707.

Previously, the two morphs were considered to be different species, *Oedothorax gibbosus* (Blackwall 1841) and *Oedothorax tuberosus* (Blackwall 1841), that could only be distinguished on the basis of the morphology of the males. However, De Keer & Maelfait (1988) proved the male dimorphism in *Oedothorax gibbosus* when both morphs hatched from one cocoon collected in the field. The terminology of the old species names and the new male morph names refers to the dorsal cephalic differentiation of the male spiders.

*Oedothorax gibbosus* is not the only spider with a male dimorphism. According to Roberts (1987), in the subfamily Erigoninae there are three other dwarf spider species in Great Britain with a male dimorphism. In each of these species, the male morphs were previously considered as separate species: *Troxochrus scabriculus* (Westring 1851) and *Troxochrus scabriculus* f. *cirrifrons* (O.P.-Cambridge 1871); *Diplocephalus connatus* (Bertkau 1889) and *Diplocephalus connatus* f. *jacksoni* (O.P.-



Figures 1–3.—Carapace of 1. gibbosus morph male, 2. tuberosus morph male and 3. female of *Oedothorax gibbosus*.

Cambridge 1903); *Dicymbium nigrum* (Blackwall 1834) and *Dicymbium nigrum* f. *brevisetosum* (Locket 1962). The jumping spider *Maevia inclemens* (Walckenaer 1837) is also characterized by two male morphs; the morphology and courtship of these male morphs are so different that one would think that they belong to two different spider species (Clark & Uetz 1992, 1993).

The elaborate structures present on the head of gibbosus males also occur in the males of many erigonine and other spider species. They have been analyzed morphologically for several species (Blest & Taylor 1977; Heinemann & Uhl 2000; Hormiga 2000; Huber 1997; Lopez 1976, 1987; Lopez & Emerit 1981; Meijer 1976; Schaible et al. 1986; Schaible & Gack 1987; Schlegelmilch 1974; Vollrath 1977). Schaible et al. (1986) suggests that the primary function of the male head structures in these erigonine spiders is to fix the position of the female during copulation. Their associated exocrine glands produce secretions, which females ingest during courtship and/or copulation. Schaible et al. (1986) were the first to suggest that the hairy groove in the gibbosus morph probably secretes a fluid that is important for the so-called gustatorial courtship, with the probable uptake of secretions by the female during courtship.

In order to observe and describe the normal courtship between a gibbosus male and *O. gibbosus* female as well as a tuberosus male and *O. gibbosus* female, we introduced a male spider into a vial (size: 5 cm diameter and 2.5 cm height) with a thin bottom of plaster containing the *O. gibbosus* female. The females had lived in these vials since they were first juveniles and had built a small web when a male of either morph was introduced. After

the introduction of the male we observed the interactions for next 2 hours. We have observed over 100 courtships.

Typically, when a tuberosus male was placed in a vial with a female, the male moved his abdomen up and down, and approached the female. Sometimes the male cleaned his palps or moved in circles or in figure eight forms while moving his abdomen up and down. Sometimes these circles were around the female, but this was mostly not the case.

When a gibbosus male was placed with a female, he performed the same courtship behavior as described above, but gibbosus also exhibited the so-called gustatorial courtship. The gibbosus male approached the female or visa versa and allowed the female to insert her chelicerae into the hairy groove. Of the two morphs of *O. gibbosus* only the gibbosus male performed such gustatorial courtship; during this courtship the female exhibited movement of the chelicerae that appeared to be feeding behavior. Heinemann (1998) also studied this courtship behavior in this species.

Following courtship in both morphs, from a face-to-face position, the male shifted his cephalothorax underneath that of the female. In that way the two palps could easily reach the epigynum and the male inserted one or both palps successively. In the case of the gibbosus male, the transition of gustatorial courtship to copulation happened smoothly or with a break between courtship and copulation. During copulation most females removed their chelicerae from the hairy groove of gibbosus male. Fixation of the position for copulation as suggested by Schaible et al. (1986) is thus not the most important function of the male head structures of the *gibbosus* morph male. This is in contrast with other dwarf



Table 1.—First experiment in which an *Oedothorax fuscus* male or female was added to a pair consisting of an *O. gibbosus* female and a tuberosus male held in a small arena. The individuals between which courtship and copulation occurred and the duration of the copulation are given in the third and fourth column. The duration of the courtship is not given because this courtship was often interrupted. There were no interactions between the *O. fuscus* spider and the tuberosus male.

|   |                                            | Added                     | Courtship and<br>copulation between                                                      | Duration<br>copulation |
|---|--------------------------------------------|---------------------------|------------------------------------------------------------------------------------------|------------------------|
| 1 | <i>O. gibbosus</i> female & tuberosus male | 1 <i>O. fuscus</i> male   | tuberosus male & <i>O. gibbosus</i> female<br>tuberosus male & <i>O. gibbosus</i> female | 67 min<br>64 min       |
| 2 | <i>O. gibbosus</i> female & tuberosus male | 1 <i>O. fuscus</i> male   | tuberosus male & <i>O. gibbosus</i> female                                               | 67 min                 |
| 3 | <i>O. gibbosus</i> female & tuberosus male | 1 <i>O. fuscus</i> male   | tuberosus male & <i>O. gibbosus</i> female                                               | 66 min                 |
| 4 | <i>O. gibbosus</i> female & tuberosus male | 1 <i>O. fuscus</i> male   | tuberosus male & <i>O. gibbosus</i> female                                               | 68 min                 |
| 5 | <i>O. gibbosus</i> female & tuberosus male | 1 <i>O. fuscus</i> female | tuberosus male & <i>O. gibbosus</i> female                                               | 70 min                 |

spider species wherein there is still contact between the female chelicerae and the male cephalic structures during copulation: *Hypomma bituberculata* (Wider 1834) (Bristowe 1931), *Walckenaeria corniculans* (O. P.-Cambridge 1875) (Schlegelmilch 1974), *Diplocephalus latifrons* (O. P.-Cambridge 1863) (Schlegelmilch 1974) and *Baryphyma pratense* (Blackwall 1861) (Blest & Taylor 1977). In *Walckenaeria cuspidate* Blackwall 1833 and *Gonatium rubellum* (Blackwall 1841) such contact only appears in the courtship (Schlegelmilch 1974).

For both male morphs, a successful copulation took more than an hour (Heinemann 1998; Vanacker unpub. data), during which first the contents of one palp is pumped into the epigynum followed by the contents of the second palp. Sometimes an incomplete copulation happened and a female received sperm from only one of the palps. There was no behavioral difference between a copulation of the two male morphs. The normal copulation position of the spiders was both spiders upside down under the web, the male above the female and the pattern of successively inserting the palps was similar for both morphs (Vanacker unpub. data). Because of the relative size of the hunch and because of the preponderance of gland cells in the hunch (unpubl. data) the production of the hunch and the hairy groove is evidently a high energy-investment for the gibbosus male. We expect that the gibbosus is probably the more sexually attractive male, but additional studies are necessary to confirm this.

The two male morphs always occur together in a population, but there is a variation in the male morph ratio between populations (Maelfait et al. 1990). It has been shown that the two morphs are determined by one gene with two alleles only ex-

pressed in the male sex (Maelfait et al.1990; Vanacker et al. 2001). The observation that the two male morphs coexist suggests that their fitness must be comparable. That the two male morphs occur together in many populations implies there may be a mixed evolutionary stable strategy, a mESS (Gadgil 1972; Maynard Smith 1982; Gross 1985; Shuster & Wade 1991; Eberhard & Guterriez 1991; van Rhijn 1991; Gross 1996; Tomkins & Simmons 1996; Schlinger et al. 1999; Simmons et al. 1999). As part of a larger study comparing the two morphs and examining several fitness characteristics we compared the response of females to each morph in the presence of a congener. Because the gibbosus male is apparently making a large morphological investment in reproduction, we expected that copulation with the gibbosus male would happen more quickly than with the tuberosus male and we expected there would be no interaction with the closely related species.

To test the response of females to each morph in the presence of another species, we set up the following experiment. An *O. gibbosus* female was put in a small transparent plastic vial (height: 2 cm, diameter: 5 cm) with a wetted thin layer of plaster of Paris and allowed to build a small web. To this individual, we added either a tuberosus or gibbosus male and one additional individual of another species (*O. fuscus* male or one *O. fuscus* female) (Table 1).

When we added to a tuberosus male and an *O. fuscus* male or female to an *O. gibbosus* female, courtship and mating happened only between the *O. gibbosus* female and the tuberosus male (Table 1). This courtship and mating behavior was not dis-

Table 2.—Second experiment in which different individuals were added (as indicated in the second column) to a pair of *Oedothorax gibbosus* female and a gibbosus male held in a small arena. The individuals between which a gustatorial courtship position occurred and the duration of that interaction are given in the third and fourth column.

|   |                                           | Added                     | Gustatorial courtship posture between               | Duration |
|---|-------------------------------------------|---------------------------|-----------------------------------------------------|----------|
| 1 | <i>O. gibbosus</i> female & gibbosus male | 1 <i>O. fuscus</i> male   | <i>O. gibbosus</i> male & <i>O. gibbosus</i> female | 10 min   |
|   |                                           |                           | <i>O. gibbosus</i> male & <i>O. fuscus</i> male     | 2 min    |
|   |                                           |                           | <i>O. gibbosus</i> male & <i>O. fuscus</i> male     | 3 sec    |
|   |                                           |                           | <i>O. gibbosus</i> male & <i>O. fuscus</i> male     | 2 sec    |
| 2 | <i>O. gibbosus</i> female & gibbosus male | 1 <i>O. fuscus</i> male   | <i>O. gibbosus</i> male & <i>O. fuscus</i> male     | 5 min    |
|   |                                           |                           | <i>O. gibbosus</i> male & <i>O. fuscus</i> male     | 2 min    |
|   |                                           |                           | <i>O. gibbosus</i> male & <i>O. fuscus</i> male     | 6 sec    |
| 3 | <i>O. gibbosus</i> female & gibbosus male | 1 <i>O. fuscus</i> male   | <i>O. gibbosus</i> male & <i>O. fuscus</i> male     | 6 min    |
|   |                                           |                           | <i>O. gibbosus</i> male & <i>O. fuscus</i> male     | 4 min    |
| 4 | <i>O. gibbosus</i> female & gibbosus male | 1 <i>O. fuscus</i> female | <i>O. gibbosus</i> male & <i>O. fuscus</i> female   | 7 min    |
| 5 | <i>O. gibbosus</i> female & gibbosus male | 1 gibbosus male           | <i>O. gibbosus</i> male & gibbosus male             | 12 min   |
| 6 | <i>O. gibbosus</i> female & gibbosus male | 7 <i>O. fuscus</i> males  | <i>O. gibbosus</i> male & <i>O. fuscus</i> male     | 5 min    |
|   |                                           |                           | <i>O. gibbosus</i> male & <i>O. fuscus</i> male     | 1 min    |
|   |                                           |                           | <i>O. gibbosus</i> male & <i>O. fuscus</i> male     | 5 sec    |
|   |                                           |                           | <i>O. gibbosus</i> male & <i>O. fuscus</i> male     | 30 sec   |
|   |                                           |                           | <i>O. gibbosus</i> male & <i>O. fuscus</i> male     | 5 min    |
|   |                                           |                           | <i>O. gibbosus</i> male & <i>O. fuscus</i> male     | 1 min    |
|   |                                           |                           | <i>O. gibbosus</i> male & <i>O. fuscus</i> male     | 6 min    |
|   |                                           |                           | <i>O. gibbosus</i> male & <i>O. fuscus</i> male     | 1 min    |

turbed by interactions of the male or female of *O. fuscus*.

However, the observations with the *O. gibbosus* female and the gibbosus male were completely different (Table 2). In this case, the intraspecific courtship behavior was disturbed by interspecific gustatorial behavior and copulation could not occur. In almost all of the interactions (Table 2), gustatorial courtship postures were between the gibbosus male and the *O. fuscus* male or female. In this experiment there was only one gustatorial courtship between an

*O. gibbosus* female and a gibbosus male morph; in this case there did not follow a copulation. Curiously, apart from one normal pairing (top of table) all courtship postures were interspecific and/or intrasexual.

Finally, in the last experiment with the gibbosus morph, seven males of *O. fuscus* were introduced to make it even more difficult for *O. gibbosus* female to choose. In this experiment we expected an increase of interspecific courtships by several *O. fuscus* males; this was also the case and the gib-



bosus male could perform neither an intraspecific courtship nor copulation.

According to the lock and key hypothesis, the function of morphological differences in closely related species is the avoidance of time- and energy-expensive copulations between the species (Arnqvist 1998). A female could recognize a gibbosus morph male because of the nuptial gift in the hairy groove and can so distinguish them from males of other related dwarf spider, such as *O. fuscus*. A tuberosus morph would not need such courtship because it does not have typical cephalic structures like other related dwarf spiders and thus is already distinct from closely related species. The sexual selection hypothesis, in contrast, proposes that divergent evolution is the result of sexual selection, brought about by variation in paternity success among males. The differences in primary and secondary sexual traits between closely related species are than a consequence of this separated evolution in these reproductively separated species (Arnqvist 1998).

According to the lock and key hypothesis, the carapace structure of the gibbosus male would function to avoid meaningless sexual interactions in terms of fitness. Because of the observed interactions between gibbosus males and spiders of *O. fuscus*, this carapace structure of the gibbosus male apparently does not serve this function. This makes an alternative explanation for the evolutionary origin of these secondary sexual characters much more probable. Instead of resulting from selection due to interspecific interactions this alternative explanation tries to understand the origin of these differences in secondary sexual characters as being caused by an arms race between different genotypes of males for mating and fertilizations, thus due to a selection resulting from intraspecific interactions: sexual selection.

In the arena of sexual interaction (Alcock 1998), features can evolve by sexual selection that affect the female's (1) choice of a copulatory partner, (2) selection of sperm to fertilize her eggs and (3) production of offspring. These male traits can be of very different nature: visual, acoustic, tactile, olfactory or gustatorial and are believed to offer cues to the female on which her mate choice can be based. The males accepted for copulation or the sperm that will be selected after copulation can be expected to produce the highest number or quality of offspring. Selection should favor female recognition of cues correlated with: (1) male health, (2) the genetic quality (good genes hypothesis), (3) sexual attractiveness of the male (Fisher's runaway selection hypothesis) and (4) material benefits (e.g., help in parental care, quality territories and nutrient transfer during copulation).

Transfer of food items or essential nutrients like salt and water during or directly after courtship and

copulation in insects is called nuptial feeding (Alcock 1998). Hypotheses put forward for the current function of nuptial feeding in insects include prevention of cannibalism by females, attraction of females, copulation enticement, positioning of the female for coupling, prolongation of ejaculate transfer to counter the effects of sperm competition or paternal investment in offspring (Vahed 1998). Nuptial feeding for example happens in *Bittacus apicalis* (Mecoptera) (Thornhill 1976; Austad & Thornhill 1991) and the cockroach *Blattella germanica* (Nojima et al. 1999). A spectacular example of nuptial feeding in spiders is the male of the red back spider that after penetration of the epigynum seemingly offers itself as a prey item by putting its abdomen very close to the chelicerae of the female who sometimes feeds on her (Forster 1992; Andrade 1996). Also relatively well studied is the offering of a prey item wrapped in silk by the male during courtship in *Pisaura mirabilis* (Clerck 1757), Pisauridae (Lang 1996; Nitzsche 1999; Stalhandske 2001). The cephalic structures occurring in many male erigonine spiders have not yet been studied in behavioral ecological and evolutionary context (e.g. not mentioned in Drengsgaard & Toft 1999 or Stalhandske 2001). The above-mentioned experiments suggest they should.

The hunch of gibbosus is completely filled with gland cells with different secretions (Vanacker, unpub. data), which strengthens the possibility that these gland cells secrete more than pheromones. Similar gland cells are found in other dwarf spider species like *Diplocephalus picinus* (Blackwall 1841) (Schaible et al. 1986). Our above-cited experiments strongly suggest that these glands produce a secretion in the cephalic groove, which is attractive not only to conspecific females, but also to conspecific males and to males and females of a closely related species. However, combinations of gibbosus morph males with females and males of other erigonine genera (*Erigone* (Audouin 1826), *Gonatium* (Menge 1868)) did not lead to gustatorial behavior (Vanacker, unpub. obs.). The chemical composition of the secretion(-s) produced remains to be determined.

Sexual selection is more and more regarded as having the potential to play a major role in speciation (Panhuis et al. 2001). According to Arnqvist (1998), genital evolution is more than twice as divergent in groups in which females mate several times than in groups in which females mate only once. In *Oedothorax gibbosus* multiple mating is also common (Vanacker unpub. obs.). Sexual selection on secondary reproductive characters as in *Oedothorax gibbosus* may have been of importance in the speciation process in the species-rich genera of Erigoninae, e.g. *Walckenaeria* (Blackwall 1833), *Oedothorax* (Bertkau 1883) and *Diplocephalus*

(Bertkau 1883). We will study this last genus in this context in the near future.

Knowing the composition of the secretion of *gibbosus* might help in better understanding the function of that gustatorial courtship behavior: female attraction or copulatory enticement, prolongation of copulation or transfer nutrients to the male's offspring (paternal investment). It seems clear that *gibbosus* offers to the female a kind of nuptial gift made available in the hairy groove. The intrasexual and interspecific gustatorial courtship postures may then be interpreted as robberies of the nuptial gift.

We are indebted to Léon Baert, Lut Van Nieuwenhuysse, Domir De Bakker, Viki Vandomme and Katrijn Deroose for helping us catch the dwarf spiders in the field. This research could be realized thanks to a PhD grant of the Foundation for Scientific Research-Flanders.

#### LITERATURE CITED

- Alcock, J. 1998. Animal behavior, an evolutionary approach. Sinauer Associates Publishers, Sunderland, Massachusetts.
- Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton.
- Andrade, M.C.B. 1996. Sexual selection for male sacrifice in the Australian redback spider. *Science* 271:70-72.
- Arnqvist, G. 1998. Comparative evidence for the evolution of genitalia by sexual selection. *Nature* 393:784-786.
- Austad, S.N. & R. Thornhill. 1991. This bugs for you. *Natural History* 12:44-49.
- Blest, A.D. & H.H. Taylor. 1977. The clypeal glands of *Mynoglenes* and of some other Linyphiid spider. *Journal of Zoology London* 183: 473-493.
- Bristowe, W.S. 1931. The mating habits of spiders, a second supplement. *Proceedings of the Zoological Society of London* 4:1931.
- Clark, D.L. & G.W. Uetz. 1992. Morph-independent mate selection in a dimorphic jumping spiders: demonstration of movement bias in female choice using video-controlled courtship behaviour. *Animal Behaviour* 43:2474-254.
- Clark, D.L. & G.W. Uetz. 1993. Signal efficacy and the evolution of male dimorphism in the jumping spider *Maevia inclemens*. *Proceedings of the National Academy of Sciences of the United States of America* 90:11954-11957.
- De Keer, R. & J.-P. Maelfait. 1988. *Oedothorax gibbosus* (Blackwall) and *Oedothorax tuberosus* (Blackwall): one species. *Newsletter of the British Arachnological Society* 53:3.
- De Keer, R. & J.-P. Maelfait. 1989. Ecological backgrounds for the distribution patterns of *Oedothorax fuscus* (Blackwall) and *Oedothorax gibbosus* (Blackwall) (Erigoninae, Araneae). *Proceedings of the Symposium "Invertebrates of Belgium"*:189-192.
- Drengsgaard, I. L. & S. Toft. 1999. Sperm competition in a nuptial feeding spider, *Pisaura mirabilis*. *Behaviour* 136:877-897.
- Eberhard, W.G. & E.E. Guterriez. 1991. Male dimorphism in beetles and earwigs and the question of developmental constraints. *Evolution* 45: 18-28.
- Forster, L.M. 1992. The stereotyped behavior of sexual cannibalism in *Latrodectus hasselti* Thorell (Araneae: Theridiidae), the Australian redback spider. *Australian Journal of Zoology* 40(1): 1-11.
- Gadgil, M. 1972. Male dimorphism as a consequence of sexual selection. *American Naturalist* 106:574-580.
- Gross, M.R. 1985. Disruptive selection for alternative life histories in salmon. *Nature* 313(3):47-48.
- Gross, M.R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends in ecology and evolution* 11:92-98.
- Heinemann, S. 1998. Männchendimorphismus bei *Oedothorax gibbosus* (Blackwall) (Araneae: Linyphiidae): Morphometrie und Verhaltensuntersuchungen. Diplomarbeit der Universität Bonn.
- Heinemann, S. & G. Uhl. 2000. Male dimorphism in *Oedothorax gibbosus* (Araneae, Linyphiidae): a morphometric analysis. *Journal of Arachnology* 28:23-28.
- Hormiga, G. 2000. Higher level phylogenetics of erigonine spiders (Aranea, Linyphiidae, Erigoninae). *Smithsonian Contributions to Zoology* 609, 22 pp.
- Huber, B. A. 1997. Evidence for gustatorial courtship in a haplogyne spider (*Hedyspilus culicinus*: Pholcidae: Araneae). *Netherlands Journal of Zoology* 47(1):95-98.
- Lang, A. 1996. Silk investment in gifts by males of the nuptial feeding spider *Pisaura mirabilis* (Araneae: Pisauridae). *Behaviour* 133:697-716.
- Lopez, A. 1976. Présence de glandes tégumentaires prosomatiques chez les mâles Erigonidae (Araneae). *Comptes rendus de l'Académie des Sciences Paris* 282(D):365-367.
- Lopez, A. 1987. Glandular aspects of Sexual Biology. Pp. 121-132. *In: Ecophysiology of Spiders*, W. Nentwig (ed), Springer-Verlag, Berlin.
- Lopez, A. & M. Emerit. 1981. Le dimorphisme sexual prosomatique de *Walckenaeria acuminata* Blackwall, 1833 (Araneae, Erigonidae). *Bulletin de la Société zoologique de France* 106:125-131.
- Maelfait, J.-P., De Keer, R. & L. De Meester. 1990. Genetic background of the polymorphism of *Oedothorax gibbosus* (Blackwall) (Linyphiidae, Araneae). *Revue Arachnologique* 9(2):29-34.
- Maelfait, J.-P., Baert, L., Janssen, M. & M. Alderweireldt. 1998. A Red list for the spiders of Flan-



- ders. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie 68:131–142.
- Maynard Smith, J. 1982. Evolution and the Theory of Games. Cambridge University Press, Cambridge.
- Meijer, J. 1976. A glandular secretion in the ocular area of certain erigonine spiders (Araneae, Linyphiidae). Bulletin of the British Arachnology Society 3(9):251–252.
- Nojima, S., Sakuma, M., Nishida, R. & Y. Kuwamura. 1999. A glandular gift in the German cockroach, *Blattella germanica* (L.) (Dictyoptera: Blattellidae): the courtship feeding of a female on secretions from male tergite glands. Journal of Insect Behaviour 12(5):627–640.
- Nitzsche, R. 1999. Das Brautgeschenk der Spinne: *Pisaura mirabilis*. Rainer Nitzsche Verlag, Kaiserslautern, 254 pp.
- Panhuis, T. M., Butlin, R., Zuk, M. & T. Tregenza. 2001. Sexual selection and speciation. Trends in Ecology and Evolution 16(7):364–371.
- Roberts, M.J. 1987. The spiders of Great Britain and Ireland, 2: Linyphiidae. Harley Books, Colchester.
- Schaible, U., Gack, C. & H.F. Paulus. 1986. Zur Morphologie, Histologie und biologischen Bedeutung der Kopfstrukturen männlicher Zwergspinnen (Linyphiidae: Erigoninae). Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere (Jena) 113:389–408.
- Schaible, U. & C. Gack. 1987. Zur Morphologie, Histologie und biologischen Bedeutung der Kopfstrukturen einiger Arten der Gattung *Diplocephalus* (Araneida, Linyphiidae, Erigoninae). Verhandlungen des naturwissenschaftlichen Vereins in Hamburg (NF) (Hamburg); 29:171–180.
- Schlegelmilch, B. 1974. Zur biologischen Bedeutung der Kopffortsätze bei Zwergspinnenmännchen (Microphantidae). Diplomarbeit Universität. Freiburg: 98 pp.
- Schlinder, B.A., Greco, C. & A.H. Bass. 1999. Aromatase activity in the hindbrain vocal control region of a teleost fish: divergence among males with alternative reproductive tactics. Proceedings of the Royal Society of London Series B- Biological Sciences 266:131–136.
- Shuster, S.M. & M.J. Wade. 1991. Equal mating success among male reproductive strategies in a marine isopod. Nature 350:608–610.
- Simmons, L.W., Tomkins, J.L. & J. Hunt. 1999. Sperm competition games played by dimorphic male beetles. Proceedings of the Royal Society of London Series B- Biological Sciences 266: 145–150.
- Stalhandske, P. 2001. Nuptial gift in the spider *Pisaura mirabilis* maintained by sexual selection. Behavioral Ecology. 12:691–697.
- Thornhill, R. 1976. Sexual selection and nuptial feeding-behavior in *Bittacus apicalis* (Insecta, Mecoptera). American Naturalist 110:529–548.
- Tomkins, J.L. & L.W. Simmons. 1996. Dimorphisms and fluctuating asymmetry in the forceps of male earwigs. Journal of Evolutionary Biology 9:753–770.
- Vahed, K. 1998. The function of nuptial feeding in insects: review of empirical studies. Biological Reviews of the Cambridge Philosophical Society 73(1):43–78.
- Vanacker, D., Maelfait, J.-P. & L. Baert. 2001. The male dimorphism in the dwarf spider *Oedothorax gibbosus* (Blackwall, 1841) (Erigoninae, Linyphiidae, (Araneae): results of laboratory rearing experiments. Belgian Journal of Zoology 131(Supplement 2):49–54.
- van Rhijn, J.G. 1991. The ruff, individuality in a gregarious wading bird. Academic Press, New York.
- Vollrath, F. 1977. Zur Ökologie und Biologie von kleptoparasitischen *Argyrodes elevatus* und synöken *Argyrodes*-Arten (Araneae, Theridiidae). Dissertation Universität Freiburg.

Manuscript received 18 March 2002, revised 18 December 2002.